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ARMILLARIA MELLEA (VAHL) SACC. IN NEW ZEALAND FORESTS

PART 1

IN STANDS OF *PINUS RADIATA* D. DON IN KAINGAROA STATE FOREST

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FOREST RESEARCH INSTITUTE
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ARMILLARIA MELLEA (VAHL) SACC. IN NEW ZEALAND FORESTS

PART 1. IN STANDS OF PINUS RADIATA D.DON IN KAINGAROA STATE FOREST

1. SUMMARY

i. A survey of the incidence of Armillaria mellea was made over some 100,000 acres of Pinus radiata forest, in order to determine the degree of parasitism of the trees by this fungus.

ii. Fiftythree 0.25 acre sample plots of P.radiata, 20-28 years old, in Kaingaroa State Forest were examined during this survey.

iii. The characteristic symptoms of the saprophytic and parasitic roles of A.mellea in pine stands are described.

iv. From the evidence submitted, concerning the characters of the fruiting bodies, the pure cultures, and the decay produced, the causal fungus was identified as A.mellea (Vahl) Sacc.

v. Parasitic attack by A.mellea was not observed to occur in the stands examined.

vi. Saprophytic attack by A.mellea was observed and an estimate of its occurrence and distribution was made for the stands examined.

vii. It was found that the occurrence and distribution of A.mellea was correlated with the site quality of the stands, the overall mortality, and the "effective" stocking but was not correlated with the basal area, the occurrence of dead trees and stumps with living butts or with the 1950-51 mortality due to Sirex attacks.

viii. An estimate was made of the occurrence and distribution of long-dead trees and stumps with living cambium.

2. INTRODUCTION

A.mellea, commonly known as the "boot lace" fungus, has been observed to attack trees, both living and dead, in various parts of New Zealand. It has a world wide distribution and a seemingly unlimited host range, having been reported to attack many types of plants from giant forest trees to asparagus crowns (Seymour 1929). The life cycle of this fungus follows the pattern of a facultative parasite. It is capable of living for long periods in dead trees, roots and logs, while under favourable conditions it is also capable of attacking and killing living trees and other plants. Parasitic attacks by this fungus have been observed in New Zealand from time to time, it being noticeably more common on exotic conifers used to underplant or replace native bush or introduced hardwoods. It has also been recorded by the author, Birch (1937a, 1937b), and Brien (1939) as :-

1. Causing a heart rot of Nothofagus menziesii (Hook.f.) Oerst., Dacrydium cupressinum Soland., Podocarpus dacrydioides A.Rich.

2. Causing a root and butt rot of P.radiata, Pinus ponderosa Dougl., Pinus nigra var.calabrica (Loudon) Sohn., Pinus contorta var.latifolia S.Watson, Pinus patula Schl. and Cham., Chamaecyparis lawsoniana Parl., Pseudotsuga taxifolia Britt., Pyrus malus L. (crab apple), Rubus idaeus L. (European raspberry), Buddleia sp., and Nothofagus spp. Oerst.

3. Occurring saprophytically on all the above mentioned species as well as Larix decidua Miller, and Beilschmiedia tawa Benth. and Hook.f.

It probably occurs either parasitically or saprophytically on most of our native and exotic timber trees.

It has been stated by Hiley (1919, p.144) that in Europe, more trees die from attacks by A.mellea than through any other parasitic agency, while in America this disease appears to be less common. Boyce (1936) states that 'probably the explanation for the greater incidence of A.mellea as a parasite on forest trees in Europe than in the United States is the fact that in Europe a large proportion of the stands are either

artificially reproduced or of unnatural composition; often both. Such stands in general cannot be so thrifty as the natural forests of this country.' (U.S.A.)

Most overseas investigators who have studied this disease in forest trees have found that it is chiefly weakened trees which become attacked. In these cases predisposition was mainly caused through the trees being weakened or injured by various unfavourable physical agencies of site or silvicultural treatment, or both.

In this country, where large areas have been planted with P.radiata, it is important to ascertain in detail the present role played by A.mellea throughout these plantations. Kaingaroa State Forest, with over 100,000 acres of pure P.radiata, was selected for initial study.

Many different authorities are quoted in literature for the specific name of this fungus. (Vahl) Sacc. has been used in this paper following Hiley (1919, p.144), who maintains that Saccardo was the first authority to raise the name Armillaria to generic rank and Vahl the first to use the specific name melleus when naming this fungus Agaricus melleus.

Considerable attention was given to the identification of the fungus in its saprophytic and parasitic forms and the first part of this paper discusses their occurrence and effects.

3. OBJECTS

a. To study the role of A.mellea associated with pure stands of P.radiata, 20-28 years old, in Kaingaroa State Forest.

b. To ascertain the relationship, if any, between the parasitic attack by A.mellea with the mortality caused by Sirex noctilio F. in the same stands of P.radiata.

4. IDENTIFICATION OF THE FUNGUS

To confirm the identification of the fungus a general study was made of its field and cultural characteristics. These characteristics are described

in some detail in view of the range of symptoms to which A.mellea can give rise.

i. Characteristic Symptoms and Mode of Attack

a. Saprophytic attack.

Dead wood may become infected with A.mellea either from spores or rhizomorphs of this fungus. Under favourable conditions the airborne spores may germinate to form mycelia which infect dead wood or other dead organic matter on which the spores had come to rest. By this means new sources of infection may be established at some distance from the original source of the spores. Direct infection of a living plant by spores has not been known to occur (Butler; Jones 1949, p.909).

The rhizomorphs, which resemble black boot laces, occur in the soil and beneath the bark of attacked roots and trees. (Figs 1, R1 and 5, R2). The subterranean rhizomorphs develop from infected submerged roots, stumps or logs, from which they penetrate the soil for a considerable distance. These rhizomorphs are capable of attacking only organic matter which is in contact with the soil. For this reason infection of recently dead standing trees is effected by rhizomorphs attacking their roots. Having penetrated the roots, the rhizomorphs grow along them, mostly under the bark towards the trunk up which they may subsequently grow. As the rhizomorphs advance they infect the wood by means of numerous side branches. When conditions are very favourable for their growth and while the bark is still held securely to the wood, the rhizomorphs tend to flatten out and may join up to form a rhizomorphic sheet. This rhizomorphic sheet may form small fan-shaped patches or may completely encircle the trunk (Figs 1, R1 and 5, M).

Free rhizomorphs, which are irregularly cylindrical in form, are made up of 2 or 3 layers of hyphae. In young rhizomorphs there is a layer of free erect hyphae which are embedded in a glutinous fluid sheath and project from a compact layer forming the tough rind.

In older parts these erect hyphae disappear, while on exposure to air the tough rind becomes hardened due to the setting of the glutinous sheath. The core in young rhizomorphs is made up of loosely woven hyphae but in older parts of the rhizomorph, a central cavity appears, surrounded by a thin layer of the loosely woven hyphae. (Butler; Jones 1949, p.912: Campbell 1934).

The rhizomorphic sheets are similarly formed so that they appear in the older parts, to be made up of 2 tough layers, separated by an almost empty cavity.

The actively growing regions of both rhizomorphs and rhizomorphic sheets are white in colour and delicate in texture. With age and exposure to the air they become hardened and change through various shades of bay brown to chestnut brown and may finally become black. These older rhizomorphic sheets range from a sixteenth to a quarter inch in thickness and may be peeled off the trunk in large pieces. When dry these sheets are usually rather stiff or brittle, but they become soft and leathery after being worked with the hands for a short time, after which they very much resemble chamois leather.

Wood that is being decayed by this fungus soon becomes bounded by zone plates (Figs 1, Z and 2, Z). In cross-section these appear as black lines demarcating attacked areas of wood. These zone plates are formed of black hyphal bladder cells (Hiley 1919, p.156: Campbell 1934) which are laid down in the wood. According to some authorities (Gäumann 1950) they are capable of apical growth. Attacked wood may be divided by these anastomosing zone plates into irregular pockets 2 or 3 inches in diameter, or it may simply be bounded by one continuous zone plate with few dissecting plates (Fig. 4, Z). The zone plates appear to form a water-tight seal which makes it possible for the fungus to maintain optimum moisture for its growth within the pockets, irrespective of outside conditions. This is demonstrated by the fact that, on opening a standing pine trunk attacked by this fungus, the partly decayed wood will be found to be

oozing water even during long, dry, summer periods (Fig. 4, E). Besides providing a water seal, these plates also appear to act as barriers (Leach 1939) to other fungi that may attempt to displace A.mellea within the pockets (Fig. 4, C). It often happens that the wood in the entire outer region of a standing pine trunk will be divided into irregular shallow pockets up to 1 inch in depth, while the infected regions within the trunk, may, or may not be divided by zone plates. The tangential walls of the exterior pockets are usually continuous, one with another, forming a complete sheath encircling the trunk (Fig. 4, Z). "Boot lace" rhizomorphs and/or "chamois leather" rhizomorphic sheets may, or may not be present after the formation of this exterior layer of pockets.

In the early stages of decay the wood is very wet, yellowish in colour, with lighter yellow strands running radially through it. These yellow strands are formed by the wood rays becoming plugged with mycelium. A large amount of water is liberated as the solid wood substance is progressively broken down. This free water of decomposition gradually accumulates within the pockets so that the decaying wood appears to become progressively more moist until, in the later stages of decay, a mushy stringy yellow rot is formed. As this process continues the fibrous nature (Fig. 4, D) of the partly decayed wood disappears until all that remains is a yellow watery jelly-like substance contained in pockets with thin black walls. Finally this yellow watery jelly-like substance drains away leaving empty pockets, the walls of which consist of the initial thin black zone plates. If these pockets have initially penetrated deeply into the wood, all that remains after this final stage of decay, is a black empty "honey comb" in the shape of the piece of wood. Such black "honey comb" logs are plentiful on the ground in native bush.

As has been described, a layer of shallow pockets is usually formed in the outer regions of attacked standing pine trunks. After the contents of the pockets have drained away, the surface of the trunk will be found to be divided into empty shallow depressions bounded by raised

thin black zone plates (Figs 3, Z and 4. D). Rhizomorphs and/or pocket formation have been observed to occur as high as 20 feet up the trunk of a dead standing pine. However it is usually only the root and butt portions of a standing pine tree that become entirely decayed by this fungus. Higher up the trunk the exterior portions may reach the final stages of decay, while the interior may be only partially decayed. The cessation of this decay by A.mellea in the interior portions is probably due to slow desiccation of the wood with any further decay being caused by the invasion of the areas by other fungi more suited to dryer conditions.

Generally speaking the most favourable wood-moisture content for the optimum growth of most wood rotting fungi lies between 35-50 percent on an oven dry basis (Cartwright; Findlay 1946, p.32). Benton and Ehrlich (1941) have shown that the optimum wood-moisture content for the growth of A.mellea was about 150 percent. This is an unusually high wood-moisture content for the optimum growth of a wood rotting fungus.

Typical symptoms of a saprophytic attack of a tree by A.mellea are :-

(1) Presence of white, chestnut brown to black rhizomorphs ("boot laces") and/or rhizomorphic sheets ("chamois leather") in or beneath the bark of roots or trunk (Figs 1, R1 and 5, R1).

(2) The presence of the typical rot in the wood; watery yellow decaying wood delimited by black zone plates (Figs 1 - 4).

Symptoms (1) and (2) may occur together or separately.

Note: Wood saprophytically attacked by A.mellea in any stage of decay was found to be strongly luminous in the dark. Since it is not known which other New Zealand fungi possess this property, it cannot be said to be peculiar to A.mellea or be used as a criterion for its presence.

b. Parasitic attack.

In a living tree the roots are the initial parts to be infected by A.mellea, chiefly by means of its rhizomorphs which occur in the soil (Fig. 5, R2). Little, if any, infection of living tissues takes place directly from germinating spores (Butler; Jones 1949, p.909).

Dead subterranean stumps, logs and roots, saprophytically attacked act as the infection foci of living trees in their immediate vicinity. The soil surrounding the infection foci is permeated by the rhizomorphs which originate from the foci. These rhizomorphs are capable of penetrating directly through the sound healthy bark of the roots of living trees (Day 1927, p.16; Thomas 1934). Penetration of the bark by rhizomorphs does not, of necessity, mean that the tree is doomed. Whether or not the infected root, and later the tree trunk, become decayed depends on many factors, most of which are still largely a matter of conjecture.

Resistance to A.mellea appears to be of the nature of an antagonistic influence on the fungus exerted by the host only when the latter is in an active healthy condition. (Thomas 1934). Unfavourable site conditions, and/or silvicultural malpractices which impair the health of a tree, probably predispose trees to attack.

After the rhizomorphs have penetrated the bark of the roots of a susceptible host, they grow rapidly in the cambial regions and bring about the decay of the woody tissues. In resistant hosts the fungus causes little destruction of the inner tissues while the point of infection is readily sealed off by new cork formation (Thomas 1934).

Providing conditions remain favourable for continued attack, the rhizomorphs tend to spread out in a fan-like manner in the cambial regions and travel along the roots towards the butt (Fig. 5, M). Advance of the rhizomorphic sheets into the host tissues is preceded by the death of the living host cells (Thomas 1934). In pines particularly, copious resin flow always accompanies an attack of the living cells (Fig. 5, Ex). Some of the exuded resin solid-

ifies within the bark layers causing them to swell and crack, while the surface of the roots and butt become coated with coagulated resin intermixed with soil, organic matter and rhizomorphs (Fig.5, Co).

Injured or retarded cambial activity is readily observed in sections of living roots or collars which have been attacked for a number of years (Figs 6, 11 12 and 7, 11). Retarded cambial activity is also often noticeable, as longitudinal grooves on the butt and lower sections of the trunk immediately above lateral roots, or on portions of the butt which have been severely attacked for some years. This effect is also apparent in butt sections, when the annual increment, as depleted by the annual growth rings, is greatly reduced, or non existent on the side of the butt immediately above heavily infected tissues.

In pines the entire root system may be killed in a very short time, especially during the first few years after being planted out. In other cases the trees may survive for many years with only a few roots being killed each year until the entire root system is destroyed. On the other hand, attacked trees may develop a resistance with age, and become capable of overcoming the attack. It sometimes happens that the root collar may become infected from a single infected root or directly from subterranean rhizomorphs, in which case the remaining root system may remain free from attack and develop normally. If the tree is susceptible, and the butt is killed, then the severed root system and trunk will be invaded by the fungus (Fig. 5). In other cases, only the main root may be infected and killed, so that the lateral roots above the dead portion may take over the whole function of the root system, becoming very much enlarged for this purpose if the tree survives (Fig. 7, L).

In many cases a tree may be diseased for many years before its crown growth is affected and it eventually dies. This gradual killing is typified in pines by a decrease in height growth together with a decrease in the length of the needles produced in the last 2 or 3

successive growing seasons. This results in stunted branches and terminals on which the current season's needles may be only half or third the length of the normal 3 or 4 year old needles. The mature needles do not droop when death occurs but remain rigidly fixed to the branches; only soft new growth, if present, tends to droop. This rigid life-like habit of the majority of the dead needles gives the tree a "bottle brush" appearance, characteristic of this type of death. The needles which turn yellow and then a vivid reddish-brown do not fall readily, so that pine trees killed by A.mellea retain this reddish-brown, rigid, "bottle brush" appearance for a considerable time. Pine trees killed by this fungus and possessing the above mentioned symptoms but without the shortened needles indicates that the killing process has been more rapid.

Trees weakened by this disease frequently fall victim to some other lethal agent, particularly wind fall.

Following the death of the host the fungus continues to live within the wood as a saprophyte, thereby providing a new source of infection to the surrounding trees. The infection of the lower portion of the trunk follows very rapidly after the cambial tissues of the entire butt have been destroyed. The rhizomorphs from the butt quickly spread up the trunk beneath the bark, killing the dying cambium and invading the sapwood. There is no resin flow accompanying this "post mortem" invasion of the trunk. Rapid invasion of the dying cambium of the trunk of a recently killed tree, without resin flow, is also characteristic of an entirely saprophytic attack of a tree recently killed by some other pathogenic agent (Figs 1 - 4). For this reason the presence of active rhizomorphs or rhizomorphic sheets of A.mellea beneath the bark of a recently dead tree does not necessarily establish that this fungus was the lethal agent.

The symptoms of the parasitic attacks on conifers by A.mellea are the presence of typical rhizomorphs and rhizomorphic sheets within and beneath the bark of the roots or butt, accompanied by resin flow and injury of the growth tissues of the host (Figs 5, 6 and 7).

ii. The Fruiting Body

The following is a description of the fruiting bodies of Armillaria mellea (Vahl) Quel. by Krieger (1947).

"Cap 1 - 6 in. broad, fleshy, rather thin, except on the disk, at first hemispheric or subconic-subumbonate, then convex or nearly plane, adorned with numerous dark, hairy, evanescent squamules, especially in the center, pale-yellowish, dingy-yellowish (honey color), or reddish-brown. mostly striate on the margin, flesh whitish, taste unpleasant. Gills subdistant, emarginate, adnate or decurrent, whitish or pallid, often with rufescent spots when old. Stem 1 - 6 in. long, 3 - 10 lines thick, equal or slightly thickened at the tomentose base, stuffed or hollow when old, sometimes floccose squamose, externally fibrous, pallid or brownish. Ring thin, webby, or well developed, white, with a thick, split, greenish-yellow or olivaceous margin, sometimes much torn and disappearing. Spores white, 7.6 - 10 x 5 - 6.3 µ.

On the ground and on decaying wood of a great variety of trees, in woods, orchards and cleared lands. Late summer and autumn. Solitary, gregarious, or in clusters, sometimes of many individuals. The hairy squamules of the cap are very fine and easily brushed away, or washed off by heavy rains. ---------- If the bark of the tree on which the plants are growing be removed, blackish cords, the so called rhizomorphs, or "shoe-strings", will usually be found."

The fruiting bodies are always attached to, or originate from, rhizomorphs. The rhizomorphs may be subterranean. growing out from decaying wood in the ground; or they may be subcortical. growing beneath the bark of badly attacked living. or dead trees. For these reasons the fruiting bodies may be found on the ground at some distance from, and surrounding decaying stumps, on the butt and lower trunk of attacked trees or attached to any subterranean piece of wood decayed by this fungus. In this present survey no fruiting bodies of A.mellea

were found originating from exotic pine wood. However, the fruiting bodies have been found in Whaka State Forest attached to rhizomorphs originating from dead Eucalyptus stumps, roots and wood (Figs 9 and 10) and at Te Whaiti, from dead Dacrydium cupressinum stumps and roots. Birch (1937b) also reported the occurrence of fruiting bodies of this fungus in several areas in New Zealand. As far as is known, the fruiting bodies have not been observed to occur attached to rhizomorphs from P.radiata wood in this country.

The fruiting bodies found by the author differed in only one respect from the description given by Krieger (1947) and others. The difference was in the type of gills, which were sinuately joined to the stem, while in all descriptions they are described as being adnate to slightly decurrent. The sinuate gills are shown in Figs 9 and 10.

The fruiting bodies artificially cultured by Birch also appear to have sinuate gills as seen in his photographs.

iii. In Culture

This fungus was isolated from the typical rot of both parasitic and saprophytic origin, from rhizomorphic sheets, from the context of the fruiting bodies, and from spore masses, on Bacto 3 percent malt agar, pH 5.5. The morphological characters of these cultures were similar, and consistent with the cultural descriptions of A.mellea given by Nobles (1948) and Cartwright and Findlay (1946, p.61). The following is a morphological description of the cultures of Armillaria mellea (Vahl) Quel. by Cartwright and Findlay (1946, p.61).

"Fungus in culture:

A.mellea produces a very characteristic growth in culture. From the point of inoculation it spreads slowly, forming at first colourless, appressed mycelium which usually develops into a compact, tightly woven, rather brittle skin. This skin very soon becomes hazel and then a very dark reddish-brown, although the growing margin remains light-coloured. Little tufts of soft light pinkish-brown mycelium may sometimes develop later on

skin. If the fungus is growing at all vigorously, root-like branching rhizomorphs are produced; these may remain light-coloured when submerged in the medium, but darken as soon as there is any tendency for it to dry out. Under the microscope the colourless hyphae are seen to have thin walls, their diameter averaging 3-5 µ. They bear occasional expansions and short swollen side-branches, but clamp connections have not been observed. The brown skin consists of a kind of "pseudoparenchyma" built up of swollen hyphae, which appear as thick-walled bladder- or dumb-bell-shaped cells up to 25 µ in diameter. These are dark yellow-brown in colour and resemble the tylosis-like swellings seen in the black zones in the wood decayed by A.mellea. ---------- Under certain circumstances the mycelium becomes luminous and the decayed wood may also exhibit luminosity."

Nobles (1948) writes - "Cultures of Armillaria mellea may be readily recognised on the basis of macroscopic appearance alone, their reddish-brown crustose areas, their rhizomorphs, and their frequent luminosity of young actively growing colonies providing a group of characters unique among the (268) species studied."

Richards (1942) writes that, of the fungi she has studied, Clitocybe tabescens (Scop.) Bres. is the only other fungus in America which produces similar rhizomorphs to those produced by A.mellea in artificial culture. Separation of the two cultures is made by an examination of them in the dark, when she found that "Armillaria mellea is always luminescent while Clitocybe tabescens is not."

Panus stypticus luminescens (Bull.) Fr. is the only other fungus reported to produce cultures exhibiting luminosity (Macrae 1942). In all other respects the cultures of P.stypticus luminescens differ from those of A.mellea.

All cultures of A.mellea made from both parasitic and saprophytic forms, from fruiting bodies and spores, were found to luminesce in the dark. Wood decayed by this fungus is also luminous.

In addition to cultures similar to those described by Cartwright and Findlay (1946), some cultures initially formed a dense erect white cottony mycelium on and surrounding the inoculum. This mycelium later became appressed with the formation of the brittle crust and rhizomorphs. Benton and Ehrlich (1941) describe 3 types of cultures, 2 of which have been described above, the third, which was not observed during this present study, produces a thin mycelium without rhizomorphs. All our cultures produced characteristic rhizomorphs to a greater or lesser degree (Fig. 8).

iv. Diagnostic characteristics

The above discussion establishes with reasonable satisfaction that the fungus dealt with is A.mellea (Vahl) Sacc., as typified by the following characters:

a. The presence of typical symptoms of both parasitic and saprophytic attacks accompanied by the characteristic subterranean and subcortical rhizomorphs.

b. The production of typical rhizomorphs in all pure cultures isolated.

c. The property of luminosity exhibited by both cultures and attacked wood.

d. The occurrence of the typical fruiting bodies from the rhizomorphs, with the expressed qualifications of sinuate gills instead of adnate or decurrent.

Artificial production of the fruiting bodies in pure culture on radiata pine wood blocks was unsuccessful.

FIELD METHODS

Fiftythree 0.25 acre sample plots were used in this survey. These had been established in 1950 to investigate the mortality of P.radiata brought about by a severe epidemic of S.noctilio in Kaingaroa State Forest. One sample plot had been established for every 2,000 acres of P.radiata. The plots were suitably located throughout the plantations so that the princi-

pal age classes and combinations of site and stocking were sampled. Although these plots were not strictly a random sample, they may be considered to be fairly representative of the area (Ure 1952).

During June and July, 1951, 25 of these plots were mapped on a 1 ft to 1 in. scale. The basal position of each tree, living or dead, and each stump was plotted and numbered. Tree mortality, during 1950-51, resulting from the attacks of S.noctilio, was noted.

Dead and dying trees were examined for the presence of the characteristic symptoms of either parasitic or saprophytic attack by A.mellea. This examination was carried out by barking the trunk from approximately 6 in. below ground level up to breast height, and also from any readily accessible roots.

The presence of living cambium in the butts of trees, and stumps, which had been dead a year or more, was also noted.

The trees in the remaining 28 plots were examined solely for the presence of A.mellea. The tree diameters for all plots, and the basal areas for the 28 plots superficially examined, were obtained from the 1951 remeasurement carried out in connection with the study of the mortality due to S.noctilio.

6. RESULTS

1. Description of the Stands

The pure stands of P.radiata which were sampled in this survey, ranged between 20-28 years of age. They had been established on an undulating plateau (from 750-2 250 ft above sea level) in pumice country that had carried a natural scrub vegetation consisting chiefly of manuka (Leptospermum scoparium Forst.) and bracken (Pteridium esculentum (Forst.f.) Diels) on the better sites, and monoao (Dracophyllum subulatum Hook.f.) and Ion cespitose Forst. tussock on the poorer sites.

The soil of this area is described as intrazonal, made up of strongly leached yellow brown pumice soil (Map ref: S.B.280, Soil Bureau 1948).

The soil has been formed from successive layers of volcanic ash. At various depths, a compacted layer is present in the depressions throughout the area, being only 6 to 9 in. below the soil surface in the Site III frost flats.

The soil is acid in reaction, most layers having a pH of about 5.3 while the surface humus zone has a pH of about 4.9

The original spacing of the trees was approximately 8 ft x 8 ft, but the effective stocking which survived 5 or 6 years after being planted out was probably considerably less in many areas. The effective stocking for each plot was estimated by counting all traceable stumps, as well as the standing living, dying and dead trees. None of the sample plots had been thinned, but some had been low or high pruned.

As was inevitable, in untended closely planted areas, considerable mortality occurred during the life of the stands. Except for the early mortality, which probably resulted from frost and deer damage followed by attack by Diplodia pinea (Desm.) Kickx and/or Phomopsis strobi (Syd.) (Birch 1937a), the bulk of the mortality has probably resulted from attacks by S.noctilio (Rawlings 1952). This insect reached its highest epidemic proportions in 1949, following a severe drought in 1946. The mortality that occurred from 1946 to 1951, due to S.noctilio, represented a medium thinning which has resulted in much healthier conditions throughout these stands than existed in 1946 (Rawlings 1952).

ii. Presentation of Data

Table I summarises all the relevant data obtained for the trees in each of the 53 plots, 25 of which were examined in detail while the remaining 28 were only examined for the presence of the fungus.

The site quality of the plots was allocated by Ure (1952) as defined by Ure (1950). Three main site classes were recognised in this area for P.radiata, using the variation in the natural vege-

tation as the indicator of site quality. Close correlation was found to exist between height growth in existing stands and the composition of the adjoining natural vegetation.

TABLE I.

Plot No.	Year planted	Living trees			Dead trees			Effective Stocking	B.A. of dying trees 1951
		Basal Area	No. of trees		No. of trees				
			D.S. 1951	T.	T.	A.S.	B.L.		
Site I.									
1144	1923	185	10	136	280	48	72	416	9
(1212)	1926	179	8	132	168	*	-	300	
1215	1926	188	6	136	356	64	36	492	1
(1264)	1927	145	0	84	216	*	-	300	
(1003)	1927	201	20	172	364	*	-	536	
(1009)	1927	190	24	152	288	*	-	440	
(1201)	1927	170	16	124	76	0	-	200	
(1189)	1928	202	40	180	56	*	-	236	
49	1928	161	56	200	384	8	84	584	34
(118)	1928	145	36	152	324	*	-	476	
(30)	1928	183	36	160	104	*	-	264	
(1235)	1931	186	28	120	144	*	-	264	
Site II.									
1119	1925	253	6	172	64	0	52	236	6
(1219)	1926	152	8	124	400	*	-	532	
1058	1926	236	0	192	256	0	136	448	0
1256	1927	147	0	128	416	16	100	544	0
1029	1927	286	16	216	100	0	76	316	13
35	1927	175	52	224	508	4	152	732	28
(54)	1928	228	44	224	280	*	-	504	
61	1928	235	16	200	136	0	28	336	5
145	1928	195	16	164	144	8	44	308	11
(117)	1928	231	56	200	180	*	-	380	
(140)	1928	180	28	188	156	*	-	344	
133	1928	228	64	288	108	0	28	396	38
107	1928	199	4	112	28	0	12	140	1
(104)	1929	183	14	228	120	*	-	348	
174	1929	258	37	288	216	24	64	504	26

Plot No.	Year planted	Living trees			Dead trees			Effective Stocking	B.A. of dying trees 1951
		Basal area	No. of trees		No. of trees				
			D.S. 1951	T.	T.	A.S.	B.L.		
Site II. (Contd)									
361	1929	151	45	196	300	0	108	496	36
(391)	1929	170	20	124	12	0	-	136	
(179)	1929	206	0	104	8	0	-	112	
(282)	1929	256	8	224	128	*	-	352	
201	1930	175	6	164	28	4	20	192	3
196	1930	218	24	140	208	0	108	348	15
338	1930	193	0	132	44	0	214	176	0
335	1930	163	4	100	64	0	32	164	1
523	1931	266	12	384	172	16	96	556	5
290	1931	256	4	292	300	12	132	592	2
Site III.									
159	1928	204	0	156	184	0	76	340	0
(447)	1929	246	16	320	72	0	-	392	
171	1929	162	42	192	244	0	172	436	31
401	1929	221	20	296	72	0	40	368	16
(262)	1929	211	28	200	72	0	-	272	
(297)	1929	149	0	112	12	0	-	124	
(445)	1929	56	0	44	0	0	-	44	
(311)	1930	210	0	188	60	0	-	248	
242	1930	207	8	160	20	0	4	180	3
(342)	1931	212	32	300	168	0	-	468	
589	1931	226	0	292	140	0	52	432	0
(600)	1931	228	9	352	132	0	-	484	
(460)	1931	209	10	284	104	0	-	388	
(494)	1931	101	0	60	0	0	-	60	
(501)	1931	122	0	64	0	0	-	64	
(532)	1931	177	0	236	4	0	-	240	

Legend: All figures shown on a 'per acre' basis.

Basal area - Is the sum of the basal areas of the living trees as in June-July, 1951, and does not include the basal areas of the dying trees at that time.

D.S. 1951 - Trees considered to be dying or dead from the attacks of S.noctilio during the previous 12 months.

T. - Total.

A.S. - Saprophytic attack by A.mellea.

B.L. - Trees with crowns that had been dead a year or more and stumps in which the whole or part of the cambium at the base of the trunk was living. These trees and stumps were noted as "butt living".

(Plot No.) - The bracketed plot numbers indicated that these plots were not mapped but only examined for the presence of A.mellea. The data for these plots were obtained from the 1951 remeasurement, recorded by Ure (1952).

* - Noted but not enumerated.

iii. Occurrence and Distribution of A.mellea.

During this survey over 2,000 dead trees, dying trees, and stumps, were examined for the presence of the characteristic symptoms of attack by A.mellea.

a. Parasitic Attack

Positive characteristic symptoms of parasitic attack were not observed, although 2 instances were found in which the symptoms were doubtful. These were 2 stumps in which half the stump was still living while the remaining half was attacked by this fungus. However, there were no symptoms present to show whether the dead portions had been attacked before or after they had died. There was a slight amount of resin flow from the line of junction of the living and infected areas but the flow was very slight compared with the amount of resin usually produced when living tissues of P.radiata are attacked by this fungus.

The methods used during this survey prevented the underground root systems of the dead and dying trees from being examined. However, considering the number of trees examined, and the methods used, it was thought that some trees showing the characteristic symptoms of parasitic infection about their surface roots, collars, and butts, would have been observed had A.mellea been parasitically active in any quantity. Symptoms of parasitic infection were not observed on any of the infected trees. It would therefore appear, that A.mellea was not active as a parasite in the 20-28 year old stands of P.radiata in Kaingaroa State Forest.

b. Saprophytic Attack

A.mellea was found to be active in some areas of the stands examined, and appeared to be purely saprophytic in all the infected trees and stumps in which it was observed.

(1) The number and percentage of plots infected.

A summary of the number and percentage of plots with, and without, A.mellea is contained in Table II.

TABLE II.

Incidence of A.mellea

Site	Armillaria mellea	No. of plots	Percentage of plots
I	Present	11	92
	Absent	1	8
II	Present	13	52
	Absent	12	48
III	Present	0	0
	Absent	16	100
All sites	Present	24	45
	Absent	29	55

It is significant from these figures that A.mellea was more common in Site I than in Site II, while it was entirely absent from Site III stands.

(2) Percentage average of dead trees infected.

From the analysis of the data for the incidence of infection within the 25 plots examined in detail, the following figures were significant -

(a) The percentage averages of dead trees infected for the plots in which Armillaria was present were as follows :-

Site I. 3 plots 12 percent of dead trees infected.

Site II. 7 plots 4.5 percent of dead trees infected.

Site III. 0 plots 0 percent dead trees infected.

(b) The percentage averages of dead trees infected for the 25 plots within each site class were as follows :-

Site I. 3 plots 12 percent of dead trees infected.

Site II. 17 plots 3 percent of dead trees infected.

Site III. 5 plots 0 percent of dead trees infected.

(c) All sites: 25 plots 4.3 percent of dead trees infected.

(d) From the above analyses it would appear that site quality is correlated with the incidence of A.mellea and that the better sites favour the occurrence of A.mellea as a saprophyte of dead and dying trees.

iv. The Correlation of Various Factors with the Occurrence of A.mellea

a. Site quality.

From the above analysis the occurrence of A.mellea appears to be correlated with the site quality of the stand.

Since A.mellea was found to be absent in such a small percentage of plots in Site I and found to be entirely absent from Site III. it is not possible to analyse the site differences of any factors within these sites in relation to the incidence of A.mellea. However, a statistical analysis has been made of the data obtained for various factors for the Site II plots, and all plots ignoring site, in relation to the incidence of A.mellea.

A summary of the data for some of the various factors obtained from the 53 plots is presented in Table III.

TABLE III.

Correlation of Various Factors with the Occurrence of A.mellea.

Site	A.mellea	No. of plots	Average actual mortality per acre	Average effective stocking	Average B.A. per acre (living trees)	Average % total mortality
I	Present	11	244	392	179	59
	Absent	1	76	200	170	38
II	Present	13	212	429	208	46
	Absent	12	111	275	211	37
III	Present	0	0	0	0	0
	Absent	16	184	284	184	21
All sites	Present	24	227	411	194	52
	Absent	29	93	277	194	27
All sites	Present & Absent	53	158	338	194	38

b. Effective stocking.

An analysis of the figures in Table IV shows that the difference between the average effective stocking for Site II plots and for all plots with and without, A.mellea was highly significant. It would therefore appear that the effective stocking is correlated with the incidence of A.mellea, in that it is more likely to be present in the stands where the effective stocking was highest.

c. Total actual mortality.

For Site II plots, the difference between the average number of dead trees per acre with, and without, A.mellea is significant at the 5 percent level of probability. The difference is highly significant for these figures for all plots, ignoring site qualities. It would therefore appear, that the incidence of A.mellea is correlated with mortality, in that it is more likely to be present in those stands where the greatest overall mortality has occurred from any cause.

d. Percentage mortality.

For Site II plots the difference between the average percentage mortality with and without A.mellea is significant at the 10 percent level of probability. It would therefore appear that percentage total mortality is not correlated with incidence of A.mellea.

e. Basal area.

The mean basal areas per acre of the living trees for Site II plots, and all plots ignoring site, with, and without, A.mellea were not significantly different.

It would therefore appear that the incidence of A.mellea is not correlated with the basal area per acre.

f. 1951 mortality due to attacks by S.noctilio.

The figures presented in Table IV are the average basal area per acre, and the average

number of trees per acre killed due to Sirex during 1950-51, for the 25 plots with, and without, A.mellea.

TABLE IV.

A.mellea	1950-51 Mortality due to Sirex.	
	Average basal area/ acre	Average No. of deaths per acre
Present	10.1	16.3
Absent	11.0	16.6

The mean basal areas per acre, and the mean number of trees per acre killed during 1950-51 due to S.noctilio. for all plots ignoring site, with, and without. A.mellea are not significantly different. It would therefore appear that the incidence of A.mellea was not correlated with the mortality due to attacks by S.noctilio during 1950-51.

g. Living cambium in dead trees and stumps.

(a) The mean number per acre of dead trees and stumps with live cambium, all plots included disregarding site quality, with, and without, A.mellea is 72 and 68 respectively. The difference between these figures is not significant. It would therefore appear, that the incidence of A.mellea is not correlated with the incidence of dead trees, and stumps with living cambium.

(b) The mean number of dead trees and stumps per acre, with live cambium was 66 which represented 37 percent of all dead trees and stumps.

(c) For all plots ignoring site quality. the average percentages of dead trees and stumps with live cambium was 35 percent with. and 47 percent without, A.mellea. The difference between these figures is not significant. It would therefore appear, that the

incidence of A.mellea was not correlated with the percentage of dead trees and stumps with live cambium.

(d) The average percentage of dead trees and stumps with living butts for the 25 plots were Site I 19 percent, Site II 48 percent and Site III 41 percent. Here there is a suggestion that the site quality of the stand may be correlated with the percentage of dead trees and stumps with live cambium. The difference between these figures is not quite significant at the 5 percent level of probability.

7. CONCLUSIONS

On the facts gained during this survey it is thought that A.mellea was not active to any appreciable degree as a parasite of P.radiata, 20-28 years old, in Kaingaroa State Forest. However, this fungus is present in many areas as a saprophyte of dead trees and stumps and is, therefore, a potential danger as a parasite.

As a saprophyte it was found to be more common in Site I than in Site II, and entirely absent from Site III stands. Site I stands, on the average, carry the greatest number of dead trees and stumps per acre and had the largest effective stocking per acre; both factors presumably are interdependant. These facts suggest that stands on the better sites provide a greater food source for saprophytic A.mellea, so that it may be expected that this fungus would be more common on the better sites. However, this does not explain the complete absence of A.mellea in Site III where, although there were, on the average, fewer dead trees, there were in some plots still a considerable number of them.

The initial infection potential, presumably from air-borne spores, is the same for all parts of the plantation.

If therefore, there is food present in the form of dead trees and stumps on these poorer sites and the infection potential is similar for all stands, then some other factor or factors must be responsible for the complete absence of A.mellea on these poorer sites.

No evidence was obtained as to the nature of these factors.

A satisfactory answer has not been found for the question: Why is A.mellea acting only as a saprophyte in these stands, especially when it is considered that they are not in a hygienic condition, and that this tree species is considered (Day 1927, p.17) to be particularly susceptible to root rot by this fungus ? It is suggested that in this instance the answer is more concerned with the degree of virulence on the part of the fungus than with the natural or induced resistance of the trees. There is some evidence, however, gained from general observations in other stands, that with age, P.radiata may develop an active resistance to attack by this fungus.

This induced or natural active resistance may develop to such a degree that at a certain age the tree may overcome this disease organism within its tissues and recover full vigour. This might indicate that, although A.mellea is present in Kaingaroa State Forest as a saprophyte, the living trees may have reached an age when they are no longer seriously affected by this parasite. In areas where A.mellea is strongly established, the second rotation of P.radiata may not escape so lightly.

A subsidiary conclusion may also be drawn from the facts gained during this survey. It is considered that, from observations in the field. the presence of living cambium in the butts of long-dead trees, and in stumps is due to their being root-grafted to neighbouring living trees. A high percentage (37 percent) of the dead trees and stumps were found to possess living cambium; this figure being an average percentage for the whole area sampled, ignoring site classes.

From the evidence submitted in this paper, no connection could be found between the occurrence and distribution of A.mellea and the 1950-51 mortality caused by S.noctilio in the stands of P.radiata examined. It is therefore suggested, that A.mellea, as it occurs in the stands examined, is not active in predisposing the trees to attack or death due to attack by S.noctilio.

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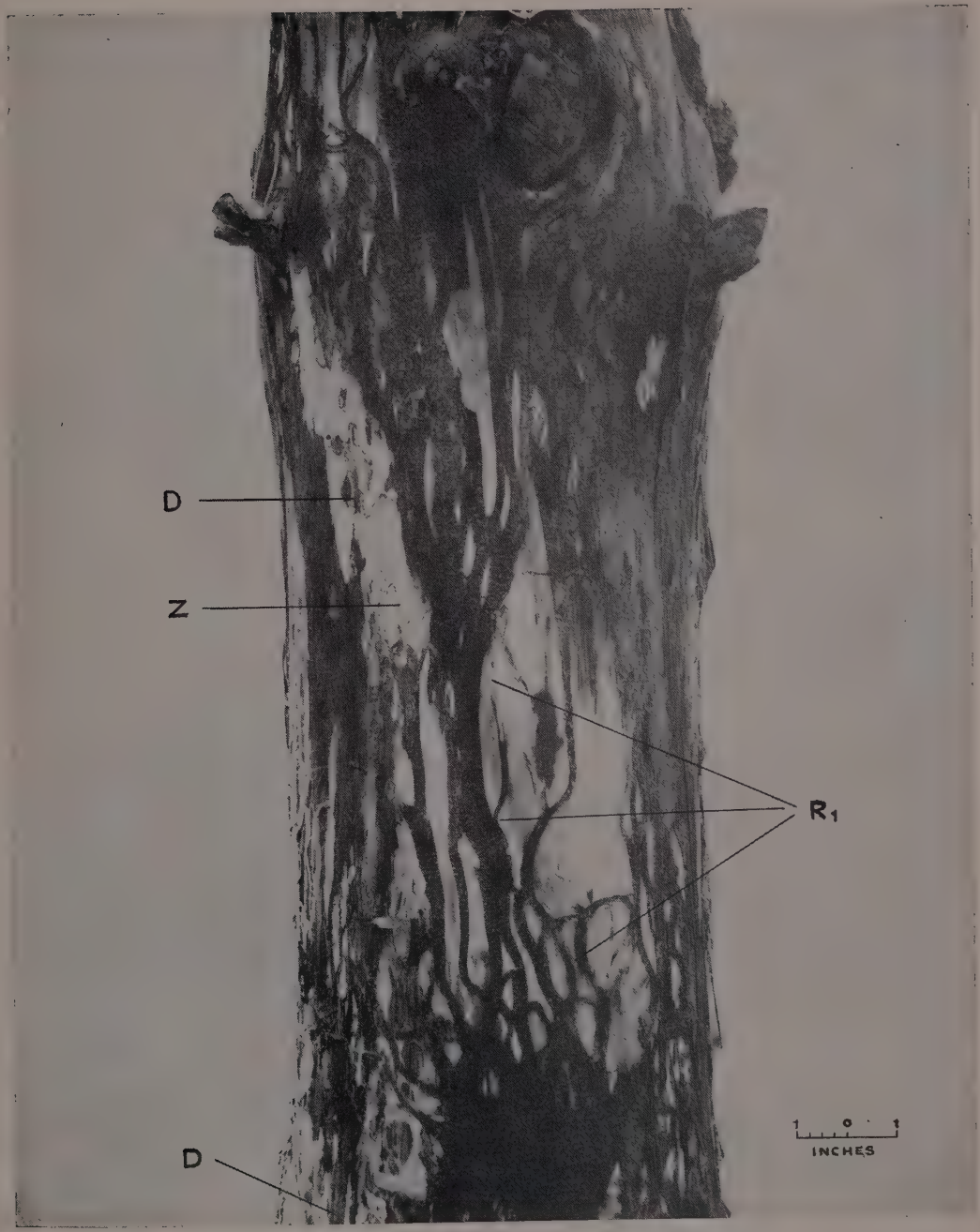

Fig. 1.– Lower portion of trunk of *P. radiata* showing subcortical rhizomorphs R1, and early stages in the decay of the wood at D with zone plates Z, caused by the saprophytic activities of *A. mellea.*

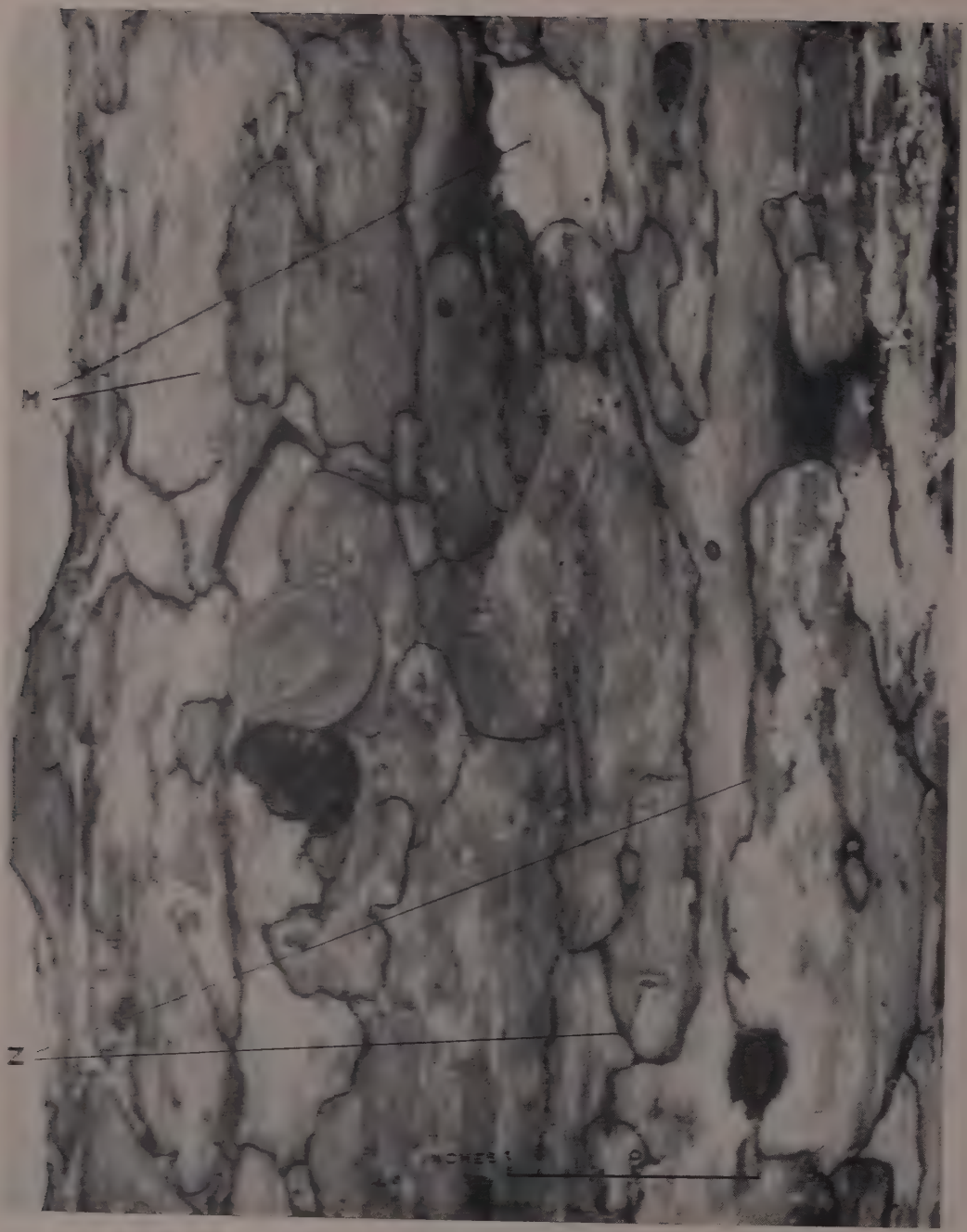

Fig. 1.—Section of P. radiata trunk with bark removed showing typical surface appearance of the outer zones of wood in upright tree A, radius. Note large irregular zonation of trunk Z, covered by white irregular streak M.

Fig. 1.—Section of *P. radiata* trunk with bark removed, showing typical surface appearance in late stages of decay by sapwood-rot fungus. Arrows point to fruiting-bodies of fungus on the wood surface.

Fig. 4.—Section through *P. radiata* trunk decayed by saprophytic *A. mellea*. Z—Continuous shallow surface zone plate. C—"Interior" zone plate separating heartwood and wood probably infected by other fungi from larger portion of trunk being decayed by *A. mellea*. D—Wood in late stage of decay. E—Wood, very wet, in an early stage of decay.

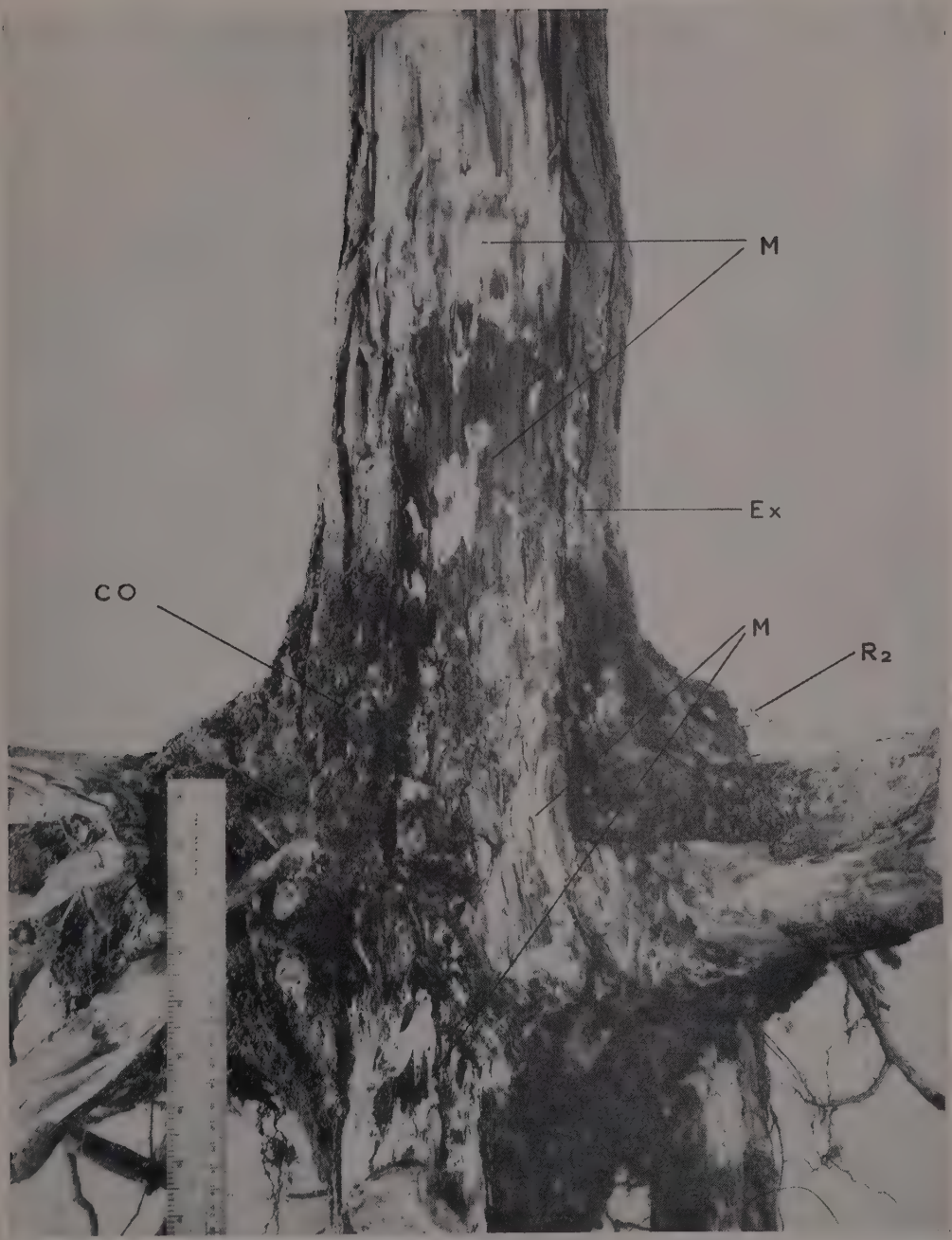

Fig. 5.—Stump of *P. radiata* parasitically attacked by *A. mellea.* Dying tree ten years old, also attacked by *S. noctilio.* Bark removed to show subcortical fungus elements. Ex—Fresh resin flow. Co—Old coagulated resin, soil, rootlets and rhizomorphs. R2—Subterranean rhizomorphs. M—Rhizomorphic sheets ("Chamois-leather").

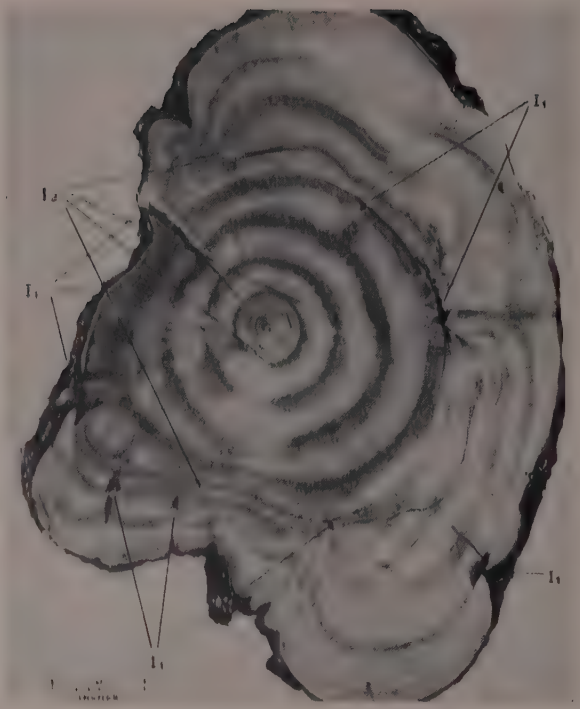

Fig. 6. Butt section, *P. radiata*, with collar infection, showing repeated injury to growing tissues. New infection in this region occurred each year except during the fifth and sixth years. I1 Infection followed by death of tissues. I2 Injury with partial or total recovery.

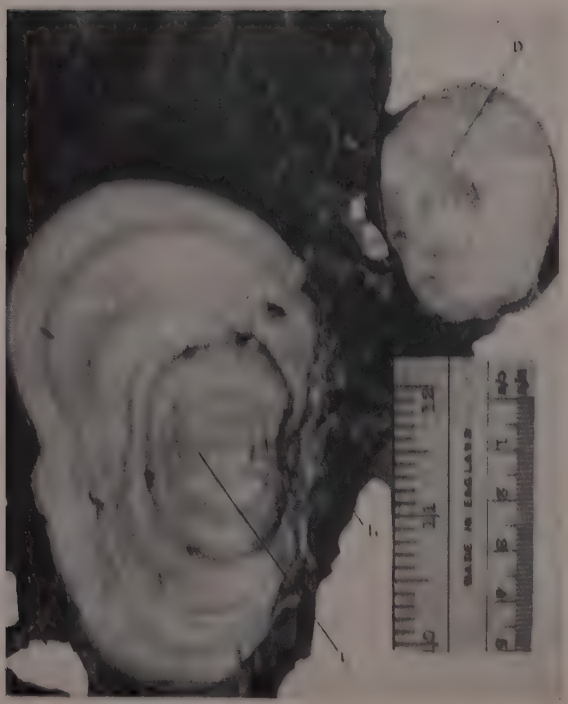

Fig. 7. Butt and root section of a severely attacked living *P. radiata* ten years old. Root I, was living but severely attacked by *A. mellea*. This fungus was still actively parasitic at I1. Root D killed in its sixth year.

Fig. 8.—Pure culture of *A. mellea* in 9 c.m. petri dish on 3 per cent malt agar after six weeks incubation at 23° c. *Note* characteristic rhizomorph development with crustose surface skin forming from the inoculum and bordering the rhizomorphs R.

Fig. 9.—Fruiting body of *A. mellea* growing from root collar of *Eucalyptus* sp. Whakarewarewa S.F. Compt 7, 1952.

Fig. 10.—Fruiting bodies of *A. mellea* originating from a subterranean root of *Eucalyptus* sp. Whakarewarewa S.F., Compt 7, 1952.

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